

EFFECT OF LOW HOST DENSITY ON OVIPOSITION BY
LARVAL PARASITOIDS OF THE ALFALFA WEEVIL¹

Robert V. Dowell^{2,3}

Abstract.—I examined the effect of different host densities at low host: parasitoid ratios (1:1–6:1) on parasitism by four larval parasitoids of the alfalfa weevil in the laboratory. The mortality inflicted was independent of changes in host density. This is due to the short handling times (<5 sec) of the *Bathyplectes* spp. and to the ability of *Tetrastichus incertus* (Ratzeburg) to parasitize only 4–5 hosts/day.

Introduction

The alfalfa weevil, *Hypera postica* (Gyllenhal) is one of the most important pests of alfalfa in the United States. Since 1957 it has been the object of a biological control effort by the U.S.D.A. and cooperating states. A total of seven parasitoid species utilizing various developmental stages of the weevil have been established and credited with reductions in alfalfa weevil numbers in the Northeast (Dysart and Day 1976).

The current emphasis on pest management models for the alfalfa weevil system has required a greater understanding of the facts influencing host-parasitoid interactions and how these interactions affect the ability of the parasitoids to stabilize host numbers (Latheef et al. 1977; Yeargan and Latheef 1977). Previous studies with *Bathyplectes anurus* (Thompson)⁴ and *Bathyplectes curculionis* (Thompson)⁴ in open-choice experiments showed no relationship between the various host densities exposed (2, 4, 8, 16 and 32) and the mortality inflicted by the parasitoids (Latheef et al. 1977; Yeargan and Latheef 1976). Thus both parasitoids appear to satisfy the definition of a density-independent mortality factor (van den Bosch and Messenger 1973) and as such are incapable of stabilizing host numbers. Yet *B. curculionis* is credited with substantial biological control of the alfalfa weevil in several sections of the United States (van den Bosch 1971; Michelbacher 1940).

Here I report the results of my investigations into the relationship between

¹ Coleoptera: Curculionidae.

² Submitted to the Graduate School of The Ohio State University in partial fulfillment of the requirements for the Degree of Doctor of Philosophy. Former address: Department of Entomology, The Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210.

³ Research partly supported by funds from the Department of Entomology, The Ohio State University. Fla. Agricultural Experiment Station Journal Series No. 989.

⁴ Hymenoptera: Ichneumonidae.

host density and parasitism by the 4 larval parasitoids of the alfalfa weevil: *B. anurus*, *B. curculionis*, *Bathyplectes stenostigma* (Thompson) and *Te-trastichus incertus* Ratzeburg.⁵ In particular, I dealt with very low host: parasitoid ratios (1:1–6:1) to determine how the parasitoids responded to changes in host density at such levels.

Methods and Materials

I reared host larvae from eggs of field collected adults (Dowell 1977a). Twenty-four hours prior to their being exposed to parasitoids, I placed 1–6 host larvae on three 7-cm-long alfalfa stems in a cotton plugged 5-cm glass vial to allow feeding and the accumulation of feces. Host larvae and their feces stimulate searching behavior in both the *Bathyplectes* spp. (Dowell 1977, McKinney and Pass 1977) and *T. incertus* (Dowell and Horn 1977). The 2nd instar hosts used for the *Bathyplectes* spp. and the 3rd instar hosts used for *T. incertus* are within the preferred host range of each parasitoid (Dowell 1977; Dysart and Day 1976).

The source and care of the various parasitoids are described elsewhere (Dowell 1977; Dowell and Horn 1976). Prior to use, each female was held for 24 hours without hosts and then 24 hours with hosts to allow for ovary maturation (all species), to prevent an excessive accumulation of eggs in the lateral oviducts of the *Bathyplectes* spp. and to allow *T. incertus* to feed on host exudates from ovipositional wounds (Dowell 1978). Each mated female was then exposed to different number of hosts daily for 2–5 successive days. Care was taken to avoid having the total number of hosts exposed exceed the expected fecundity of the parasitoid species (Dowell 1977). Host larvae were exposed to individual parasitoids in 10 × 10 × 9 cm plastic containers (Dowell 1977) for 24 hours in a Percival environmental chamber held at 21°C and 12 hour photophase. After use, all parasitoids were dissected to be certain that their ovaries were functional (Dowell 1976), and only those females with functional ovaries were included in the data analysis. A minimum of four replicates/density/species were run. After exposure the host larvae were reared until pupation to determine whether they were parasitized. The data for each host density were averaged by parasitoid species and mortality was expressed as k-values ($k = \log_{10} \text{initial \#} - \log_{10} \text{survivors}$) (Varley and Gradwell 1965). The effect of host density on mortality (k-values) was examined by use of regression analysis.

A fungal disease similar to that described by Dysart and Coles (1971) killed most of the larvae exposed to *B. stenostigma*.

Results and Discussion

Table 1 shows the results of the regression analysis of the k-values on host density for each parasitoid. There was no significant ($P < 0.05$) affect

⁵ Hymenoptera: Eulophidae.

Table 1. Results of regression analyses of k-values (y) of the larval parasitoids on alfalfa weevil density (x).

Parasitoid species	Regress. coeffs.	Intercept	Standard error of estimate	r	t-value H ₀ : b = 0
<i>B. anurus</i>	-0.01	0.39	0.24	-0.05	-0.17*
<i>B. curculionis</i>	0.04	0.14	0.18	0.31	0.05*
<i>T. incertus</i>	-0.01	0.44	0.10	-0.25	0.42*
<i>B. stenostigma</i>	0.15	0.15	0.11	0.98	5.01†

* Not significantly different from b = 0 at P = 0.05 as determined with a t-test.

† Significantly different from b = 0 at P = 0.05 as determined with a t-test. However there were only 4 data points for this analysis; one replicate at each of 4 densities.

exerted by changes in host density on the mortality inflicted by *B. anurus*, *B. curculionis* or *T. incertus*. Only the mortality inflicted by *B. stenostigma* significantly ($P > 0.05$) changed with changes in host density. However, the previously mentioned disease limited this data analysis to the 1 replicate that survived at each of 4 densities. Previously I (Dowell 1977; 1978) have shown that the biology and reproductive tactics of *B. stenostigma* differ little from its congeners. Based upon these previous studies, I feel that *B. stenostigma* probably responds to changes in host density in a manner similar to its congeners and that the small number of replicates analyzed were insufficient to show this.

The density-independent response of *B. anurus* and *B. curculionis* to changes in host density at these low host:parasitoid ratios agree with previous studies using greater ratios (5:1-100:1) (Barnety et al. 1977; Latheef et al. 1977; Yeargan and Latheef 1977). That *T. incertus* also responded in a density-independent manner is surprising since its reproductive biology differs greatly from that of the *Bathyplectes* spp. (Dowell 1978; Dowell and Horn 1977). Recent studies have shown that the field mortality inflicted by *B. anurus* and *B. curculionis* in Ohio (Lewis 1977) and by *B. curculionis* and *T. incertus* in Ontario (Harcourt et al. 1977) is independent of changes in host density.

I believe that the density-independent response of the *Bathyplectes* spp. and *T. incertus* to changes in host density have different origins but that both can be explained by the effect of several biological traits on the disc equation (1) of Holling (1959).

$$N_a = \frac{aT_t N_o}{1 + aT_h N_o} \quad (1)$$

Where:

N_a = Number of hosts parasitized
a = area of discovery

$$\begin{aligned} T_t &= \text{exposure time} \\ T_h &= \text{Handling time/host} \\ N_o &= \text{Number of hosts available.} \end{aligned}$$

The handling time for the *Bathyplectes* spp. is <5 sec/larva (Dowell 1977) making it approximately equal to zero when compared to the exposure time of 12 hr. When this happens; equation 1 can be reduced to the following:

$$N_a = aT_t N_o \quad (2)$$

The numbers of hosts parasitized now becomes a linear function of the number of hosts available as 'aT_t' is a constant in this equation. According to both this study and others cited herein, the slope of this linear function does not significantly differ from zero.

The handling time for *T. incertus* is >23 min/larva (Horn 1970) and is large enough to keep equation from reducing. When the average number of hosts at each density is fitted to the disc equation by the method described by Holling (1959) and Messenger (1968) the result is equation 3.

$$N_a = \frac{0.68 N_o}{1 + 0.07 N_o} \quad (3)$$

According to equation 3, *T. incertus* should show a density-dependent response to changes in host numbers until all the available eggs have been laid. I believe that *T. incertus* is capable of parasitizing an average of only 4–5 hosts/day. This low figure is limited in two manners. The first is that egg production in *T. incertus* is dependent upon a continual supply of proteins gathered by feeding on ovipositional wounds on the host (Dowell 1978). This combined with the low number of ovarioles/ovary (n = 12) (Dowell 1978) limit the number of eggs formed/day. In addition *T. incertus* lays an average of 5–6 eggs/host (Streams and Fuester 1967) further restricting the number of host larvae it can parasitize on a daily basis. The final result is that a density-dependent process appears density-independent due to the limited number of hosts the parasitoid can parasitize on a daily basis.

The density-independent mortality inflicted by the larval parasitoids of the alfalfa weevil, whether based upon the rapid handling time/larvae or the limited number of larvae that can be parasitized/day, make them incapable of stabilizing host numbers. While their presence does increase host mortality, they alone are not responsible for long-term decreases in host numbers.

Acknowledgments

I thank my committee, Drs. Gordon R. Stairs, David G. Nielsen and Rodger Mitchell for their help and guidance in my work, the Entomology

Department of The Ohio State University for its financial support, Drs. K. V. Yeargan, M. A. Latheef and B. C. Pass for graciously allowing me access to their data and unpublished manuscripts, and John K. Fessel, Richard J. Dysart and K. V. Yeargan for supplying me with parasitoids at various times. I especially thank my advisor and friend David J. Horn for his help, understanding and loan of his cabin throughout my graduate career.

Literature Cited

- Dowell, R. V. 1976. Non-functional ovaries in *Bathyplectes* spp. (Hymenoptera: Ichneumonidae), larval parasitoids of the alfalfa weevil (Coleoptera: Curculionidae). J. N. Y. Entomol. Soc. 94:384-5.
- . 1977. Biology and intrageneric relationships of *Bathyplectes stenostigma*, a parasite of the alfalfa weevil. Ann. Entomol. Soc. Amer. 70:845-8.
- . 1978. Ovary structure and reproductive biologies of larval parasitoids of the alfalfa weevil. Can. Entomol. 110:507-12.
- and D. J. Horn. 1977. Adaptive strategies of larval parasitoids of the alfalfa weevil. Ibid. 109:641-8.
- Dysart, R. J. and L. W. Coles. 1971. *Bathyplectes stenostigma*, a parasite of the alfalfa weevil in Europe. Ann. Entomol. Soc. Amer. 64:1361-67.
- and W. H. Day. 1976. Release and recovery of introduced parasites of the alfalfa weevil in Eastern North America. USDA Prod. Res. Rpt. No. 167, 61 p.
- Harcourt, D. G., J. C. Guppy and M. R. Binns. 1977. The analysis of intrageneration change in Eastern Ontario populations of the alfalfa weevil, *Hypera postica* (Coleoptera: Curculionidae). Can. Entomol. 109:1521-34.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. Ibid. 91:385-98.
- Horn, D. J. 1970. Oviposition behavior of *Tetrastichus incertus*, a parasite of the alfalfa weevil. J. Econ. Entomol. 63:303-4.
- Latheef, M. A., K. V. Yeargan, and B. Pass. 1977. Effect of density on host-parasite interactions between *Hypera postica* (Coleoptera:Curculionidae) and *Bathyplectes anurus* (Hymenoptera:Ichneumonidae) Can. Ent. 109:1057-62.
- Lewis, D. R. 1977. Analysis of the life table of the alfalfa weevil in Ohio. Ph.D. Dissertation, The Ohio State University.
- Messenger, P. S. 1968. Bioclimatic studies of the aphid parasite *Praon exsoletum* 1. Effects of temperature on the functional response of females to varying host densities. Can. Ent. 100:728-71.
- McKinney, T. R. and B. C. Pass. 1977. Olfactometer studies of host seeking in *Bathyplectes curculionis* Thoms. (Hymenoptera:Ichneumonidae). J. Kansas Entomol. Soc. 50:108-112.
- Michelbacher, A. E. 1940. Effect of *Bathyplectes curculionis* on the alfalfa weevil population in lowland middle California. Hilgardia 3:81-99.
- Streams, F. A. and R. W. Fuester. 1967. Biology and distribution of *Tetrastichus incertus*, a parasite of the alfalfa weevil. J. Econ. Entomol. 60:1576-79.
- van den Bosch, R. 1971. Biological control of insects. Ann. Rev. Ecol. and Systematics 2:45-66.
- and P. S. Messenger. 1973. Biological Control. In-text Educational Publishers. 180 p.
- Varley, G. C. and Gradwell, G. R. 1965. Interpreting winter month population changes. Proc. XII Int. Cong. Ent. (London) pp. 377-78.

Yeagan, K. V. and M. A. Latheef. 1976. Host-parasitoid density relationships between *Hypera postica* (Coleoptera:Curculionidae) and *Bathyplectes curculionis* (Hymenoptera:Ichneumonidae). J. Kansas Entomol. Soc. 49: 551-6.

University of Florida, Agricultural Research Center, 3205 S.W. 70th Ave., Ft. Lauderdale, FL 33314.

Received for publication May 18, 1978.